

BARK SURFACES AND THE ORIGIN AND MAINTENANCE OF DIVERSITY AMONG ANGIOSPERM EPIPHYTES: A HYPOTHESIS

D. H. Benzing*

INTRODUCTION

A number of angiosperm families have achieved the requisite adaptations to colonize forest canopy habitats and several of these have done so with considerable redundancy. Genera such as *Anthurium*, *Oncidium* and *Tillandsia* contain hundreds of arboreal members, including many with similar growth forms and what appear to be the same fundamental vegetative adaptations to canopy life. Not uncommonly, two or more taxa are so alike in appearance as to be unidentifiable without sexual material. Often groups of such species are sympatric and occupy the same kinds of bark surfaces (hosts) in apparent defiance of the prevalent notion that distinct populations must occupy separate spatial niches in order to exploit common habitats over prolonged periods of time.

If groups of sympatric epiphytes are indeed adapted to the same types of substrata, why haven't the most aggressive ones achieved unilateral dominance in given localities through competitive exclusion? On the other hand, if considerable niche overlap can exist among many closely related epiphytes with superimposed ranges, might this explain in part why so many aroid, bromeliad, orchid, etc. genera are very large, and succeed in packing numerous forest communities and even individual hosts with so many of their species?

ORIGINS OF EPIPHYTE DIVERSITY

Speciation among the larger families of canopy dwellers has been effected by a variety of mechanisms and encouraged by various circumstances, many with no relationship to habitat preference. For example, ethological phenomena have been paramount in fostering taxonomic expansion within epiphytic Orchidaceae. In addition, the epiphytic biotope is itself both spatially and temporally conducive to high rates of evolution. Forests in general, and the species of host trees within them, exhibit shifting, disjunct distributions requiring that associated populations of canopy inhabitants be fragmented or diffusely dispersed. Mounting evidence suggests that many epiphytes exhibit spotty distributions of reproducing individuals even when occupying extensive and relatively uniform forests which presumably could support larger, more evenly distributed populations (Madison, 1979; Benzing, 1981). Whatever the reasons for their patchy dispersions, precipitous genetic restructurings of the resulting small isolates by phenomena such as genetic drift, the flush-crash-founder syndrome (Carson, 1975; Powell, 1978), bottleneck effect (Nei *et al.*, 1975) and founder effects (Mayr, 1942) have probably contributed substantially to the diversity of these organisms much as the same mechanisms facilitated radiation of other taxa native to spatially discontinuous habitats (e.g., Hawaiian *Drosophila*: Carson, 1970, 1971).

In the following discussion, I do not intend to argue that the potential for niche overlap or any other particular factor has somehow directly promoted speciation among groups of epiphytes. I will suggest that by not having to partition their habitats into distinct spatial niches, certain groups of canopy dwellers have been less constrained in achieving diversity at low taxo-

*Oberlin College, Oberlin, Ohio 44074, U.S.A.

nomic levels than have many terrestrial groups endemic to more equable sites where competition is intense, patchiness and disturbance less pronounced and vascular plant diversity in general much greater than that in the epiphytic biotope.

TILLANDSIA ON TAXODIUM

The use of *Taxodium ascendens* by *Tillandsia* in southwestern Florida (Figure 1) is but one example of host sharing by many closely related and/or ecologically similar species. In the Big Cypress Swamp, *Taxodium* growing over vast expanses of thin, nutrient-deficient soil rarely exceeds heights of 6-8 meters, although individual specimens may be several hundred years old. Crowns remain uniformly sparse through maturity, exposing most of the bark surfaces of these trees to precipitation and intense diurnal illumination for unusually extended periods of time.

In all, eight species of *Tillandsia* infest *Taxodium* in these forests -- *T. usneoides*, *T. circinnata*, *T. balbisiana*, *T. fasciculata*, *T. utriculata*, *T. re-*



Figure 1. Dwarfed cypress forest in southwestern Florida.

curvata, *T. flexuosa* and *T. polystachia*. The remaining members of this genus in Florida -- *T. setacea*, *T. bartramii*, *T. valenzuelana* and *T. pruinosa* -- tend to be restricted to broadleaf hosts or better-developed stands of cypress. While some taxa are more abundant than others in some or all parts of the Big Cypress Swamp, none appear to be responsible for the absence of another on a particular support. Collectively, resident epiphytes never occupy more than a few percent of what appears to be uniformly accessible bark surface (Figure 2).

Each of the eight resident tillandsias is a drought-enduring CAM xerophyte with a weak tolerance for heavy shade. Its roots have little absorptive capacity but serve primarily as holdfasts. All are excluded from the lower levels of small, localized patches of denser broadleaf forest (bayheads) in-

terspersed through these cypress stands. All occur rooted to upright trunks of *Taxodium* as well as to larger vertical and horizontal branches. *Tillandsia fasciculata* and *T. utriculata* alone are excluded from the weakest twigs, but only because of large adult size; their juveniles occur throughout the crown. In effect, except for the constraints imposed by mass, these bromeliads are ecologically interchangeable in choice of substratum, at least when occupying dwarfed cypress supports. The dwarfed cypress crown, for its part, does not appear to be compartmented in any way that would impose a spatial segregation on an epiphyte load even if its members did vary according to shade or drought tolerances or mineral requirements. I suggest that comparable circumstances prevail in many forest canopies, and that similar ecological overlap is inherent among many of the populations of vascular epiphytes they support.

RESOURCE PARTITIONING AMONG EPIPHYTES

Resource partitioning does exist and has been documented among epiphytes of several taxonomic groups. Colin Pittendrigh (1948) was sufficiently impressed by this phenomenon to devise a formal classification comprised of three categories to distinguish the gross habitat preferences of sympatric bromeliads in Trinidad. Member species of a particular ecological category were presumed to be adapted to occupy lower, middle or upper portions of the profiles of dense forests, depending on their shade tolerance and humidity requirements. No consideration was given to possible unique, finer requirements for specific kinds of substrata that might have facilitated the coexistence of ecologically similar taxa in the same sector of a particular canopy. Sanford & Adanlawo (1973) have described how drought tolerances provided by different degrees of velamen development (numbers of cell layers) equip certain West African orchids to recruit sites with specific exposures and levels of humidity. Went (1940) was persuaded that some epiphytic orchids share common hosts by partitioning their anchorage surfaces into a series of preferred types.

Some partitioning of the bark surface is obvious even among the vascular epiphytes of *Taxodium ascendens* in the Big Cypress Swamp. The orchid *Encyclia tampensis* grows only on trunks and larger limbs, often around surface irregularities and rotted knotholes. *Cyrtopodium punctatum* and *Psilotum nudum* inhabit only deep cavities containing moist debris. Quite possibly, closer examination would reveal that some resident tillandsias live where lichens are particularly abundant or the bark surface is older and more wettable. Resource partitioning imposed by seedlings could be subtle but decisive, and its basis lost or difficult to discern by the time a specimen has reached adulthood.

COMPETITIVE EXCLUSION AND COEXISTENCE

The belief that n species cannot coexist for extended periods of time on less than n resources or, to put it more broadly, that a given number of sympatric populations must occupy the same number of distinct niches, continues to dominate biological thought in many quarters. The reasons for this notion's enduring acceptance by so many biologists as practically axiomatic are understandable, given the prominence of its proponents, the force of their arguments, and the inaccessibility of much of the supporting logic to those without considerable mathematical sophistication. Volterra (1928) gave the theory creditability and rigorous status with a workable (within certain limits) mathematical model. More recently, influential reports by several au-

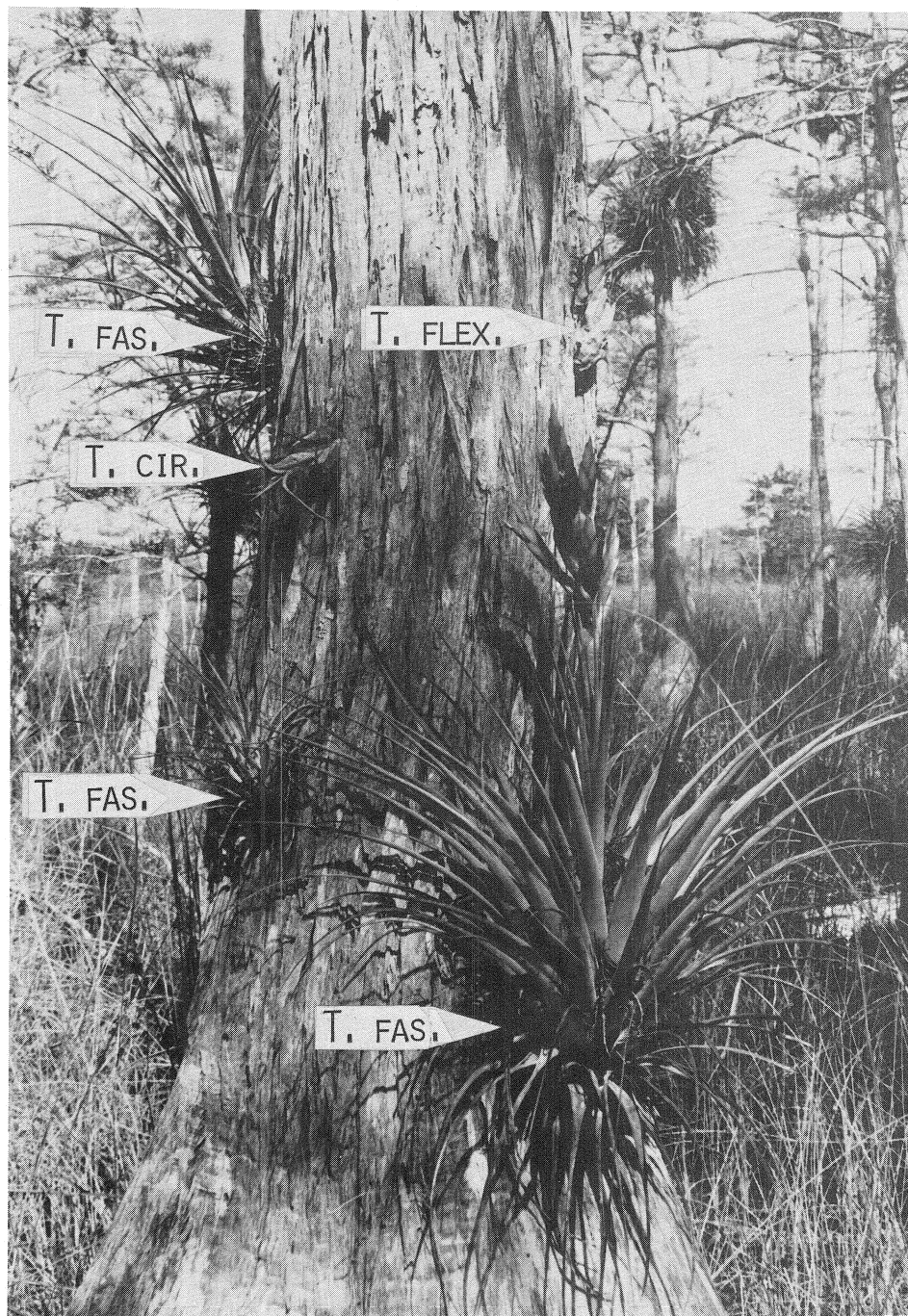


Figure 2. The bark of a dwarfed *Taxodium ascendens* hosting a mixed population of *Tillandsia circinnata*, *T. flexuosa* and *T. fasciculata*.

thors have broadened the theme (e.g., MacArthur & Levins, 1964; Levins, 1968) until now it serves as the basis of what has become known as the "competitive exclusion principle."

Empirical studies have been carried out in recent years (e.g., Hutchinson, 1961; Dayton, 1971; Sale, 1977) and theoretical models formulated (Ayala, 1969; Horn & MacArthur, 1972; Koch, 1974; Armstrong & McGehee, 1976a, b; McGehee & Armstrong, 1977) to demonstrate that two or more species can indeed coexist indefinitely on less than equal numbers of resources in homogeneous environments. Furthermore, not all participating populations need be equally effective utilizers of those shared resources to persist in intimately intermixed groups. Densities of species supported by a common resource will fluctuate in accordance with the impact of certain disturbances, most often predation and mechanical disruption of substrata. Should the densities of individuals be maintained at sufficiently low levels by these disruptive forces, no participating taxon need exclude another or be excluded itself by virtue of either great or poor competitive ability.

Some coral reefs and the intertidal zone along certain rocky shore lines are habitats deserving attention from those interested in the ecology of epiphytes. Numerous sessile plants and animals exploit these environments, populating them with a shifting mosaic of interspersed species. Competitive prowess varies among individual populations, as do their capacities to colonize and exploit vacant substrata (Dayton, 1971, 1975; Sale, 1977). Some intertidal species persist in spite of poor competitive qualities because they are able to recruit freshly exposed bare rock quickly each time wave action or other physical trauma removes patches of established, more competitive organisms. Were these disturbances less frequent, the biological diversity on such sites would be diminished since the poor competitors (in this case, the fugitive species) would be eliminated.

Guilds (collections of ecologically similar populations in the same community; Root, 1967) of certain coral reef fish exist in spite of their common habitat (space) and food preferences and, even more than intertidal inhabitants, bear a striking resemblance in certain life history characteristics to tillandsias on cypress (Sale, 1977). These fish survive in mixed populations by individually producing numerous highly mobile young over extended breeding seasons. Their planktonic larvae are readily dispersed by currents to newly opened spaces where they become sedentary. A patch of space is opened for recolonization each time a hapless guild member dies, usually at the hands (or mouth, rather!) of a predator. Considerable diversity persists on the reef because every member species of the guild participates in a kind of lottery for randomly available space in what amounts to an unpredictably disturbed, patchy environment. Competitive abilities are of little consequence since the individual who usually succeeds on a newly vacated site is the first to arrive and establish a territory, regardless of taxonomic identity.

The rocks of an intertidal community, the nooks and crannies among coral heads and the crowns of cypress bear much similarity, both in terms of the dispersion of habitable space and the dynamics of its turnover. The 8 tillandsias on dwarfed *Taxodium* in the Big Cypress Swamp would be competing for space were it not for these two factors. In the first place, the substratum of an epiphyte, being made up of small patches of bark, can be equated to the anchorage faces along a rocky shore or to the scattered volumes of habitable space on a reef. Secondly, disruptive events occur in tree crowns just as they do in intertidal and coral reef environments. Bark fragments ex-

foliate and stems detach in a pattern of disturbance which is, in effect, much like the localized destruction of rock inhabitants caused by wave action and colliding driftwood or the random removal of territorial reef fish by predators. Thus, in all three habitats, comparable constraints prevent competitive exclusion and foster high biotic diversity and long-term exploitation of a common substratum. Among epiphytes, diversity is expressed at, and restricted to, progressively finer taxonomic levels as climatic stress increases; few major families have achieved the basic adaptations required to cope with the many physical constraints on plant life inherent to arid canopy habitats (Benzing, 1978).

TWO STRATEGIES FOR HOST SHARING

Two strategies, either of which could, in theory, allow two or more populations of epiphytes to coexist indefinitely on a single host, are depicted in Figure 3. In the first case (strategy A), two sympatric epiphytes react to the surface of a common host as a patchwork of two different kinds of habitable space, only one of which is serviceable for a particular population. As generations of patches disappear and are replaced by others (sometimes in the same place, as when bark fragments exfoliate), each taxon colonizes successions of its preferred patch type. Since the participating populations have effectively partitioned the common substratum, no competition for anchorage sites will ensue. A taxon's persistence on a particular host will depend solely on its ability to sustain sufficient regenerative power to keep enough of its exclusive patches occupied.

The second strategy (B) is predicated on the notion that a group of appropriately defined species can coexist in perpetuity if they collectively exploit a common parcel of patchy but otherwise uniform space in a sufficiently weak and spatially random fashion. In this situation, all patches are interchangeable in the sense that both participating epiphytes can colonize any one of them with about equal chance of success. Note from the diagram that only a third of the patches in any generation are occupied by epiphytes. Such underexploitation of space is mandatory for the operation of this strategy. Colonization of one set of patches from the preceding one by each participant is random -- by anemochory in the case of tillandsias. It is also feeble, owing to the inability of any population to saturate the substratum with its seeds and to the low probability that a given seed will impact on a favorable site amid such a scattered array of serviceable surfaces. As long as old patches are replaced by new ones at a high enough rate, and each population remains sufficiently fecund to hold enough patches in its service, coexistence will endure. Densities of each participating population will fluctuate over time, but interspecific interference will be held to a minimum.

Patch longevity is all-important in both models. If too short relative to the time required for plants to mature and replace themselves, the site would be, by definition, intolerably disturbed for that taxon. If too long, multiple recruitments of patches by more than one epiphyte could become common enough to bring individuals of the same or different species into serious competition. Similar confrontations would ensue if members of one or more species were capable, by offshoot growth, of invading new patches from old ones, thus allowing a genet to dominate multiple generations of bark patches over large sectors of a host crown. This second possibility is precluded among air plants by their patterns and powers of asexual recruitment. All produce slow-growing, closely associated offshoots. Successive generations of asexual progeny are, in effect, obliged to occupy the parental patch.

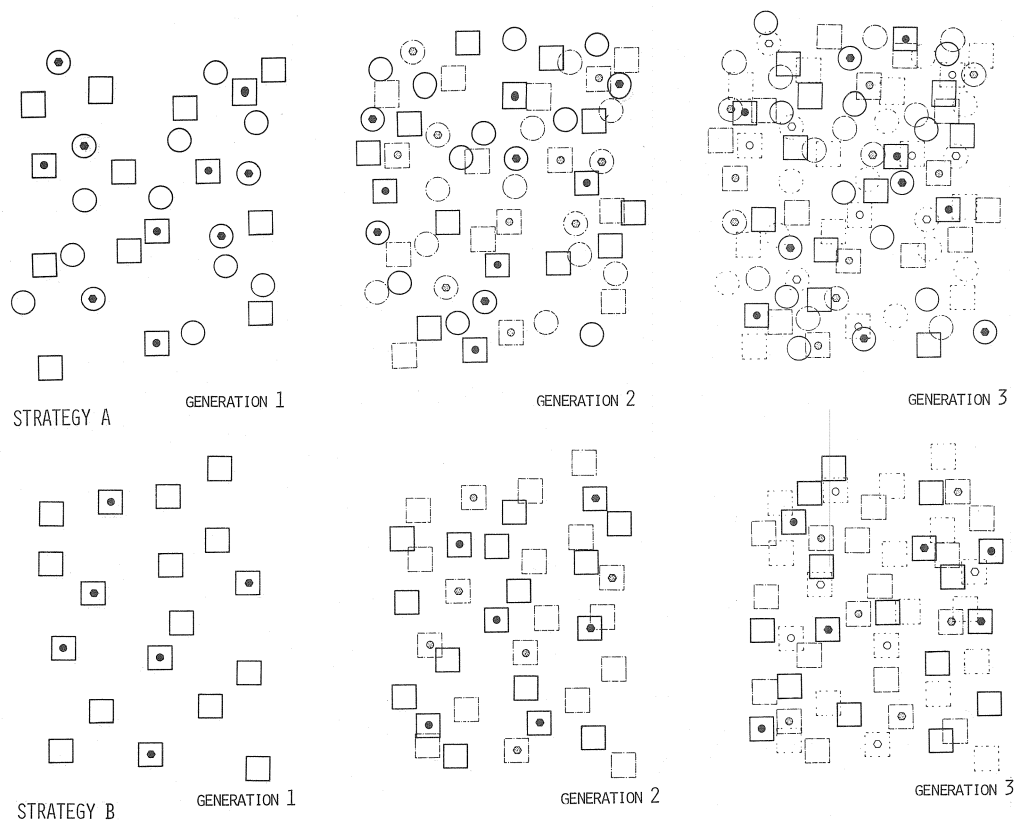


Figure 3. Two strategies for coexistence of two epiphytes on a common bark surface. Strategy A: two sympatric species with different patch preferences sharing an expanse of bark comprised of two distinct patch types, each of which will accommodate just one species. Strategy B: coexistence involving two epiphyte populations with identical substratum preferences residing on patches of uniform bark. In both cases, patch occupancy remains at 33.3% over three successive generations (frames) of patches. Solid line squares and large circles represent extant patches in each of the three frames. Solid hexagons and small circles inside extant patches represent living patch residents. Slightly broken line squares and circles with stippled residents in the second and third frames represent recently extinct patches and the epiphytes that once exploited them. Very broken line patches with open symbols in the third frames represent patches and occupants that ceased to exist two generations back. These were the extant patches and epiphytes in Frame 1.

Should a group of epiphytes be too vegetatively vigorous and fecund, or too many seedlings survive to adulthood, as may well be the case among mesic species in wet forests, coexistence according to Strategy B may be strained, if not impossible. Compared to such xeric forms as the tillandsias on Florida cypress, distributions of mesophytic epiphytes among mixed groups are likely to be more strongly influenced by competition leading to character displacement, and their spatial niches accordingly more narrow and distinct. Very close study will be required to differentiate those groups of coexisting epiphytes with seemingly identical, but in fact distinct, substratum requirements from others whose survival depends on pursuit of what can be viewed as a kind of botanical musical chairs -- one where safe sites remain numerous but have shifted their positions each time the much smaller numbers of players are sufficiently rested to get up and continue the game.

LITERATURE CITED

- Armstrong, R. A. & R. McGehee 1976a. Coexistence of two competitors on one resource. *J. Theor. Biol.* 56: 499-502.
- 1976b. Coexistence of species competing for shared resources. *Theor. Pop. Biol.* 9: 317-328.
- Ayala, F. J. 1969. Experimental invalidation of the principle of competitive exclusion. *Nature* 224: 1076-1079.
- Benzing, D. H. 1978. The life history profile of *Tillandsia circinnata* (Bromeliaceae) and the rarity of extreme epiphytism among the angiosperms. *Selbyana* 2: 325-337.
- 1981. The population dynamics of *Tillandsia circinnata* (Bromeliaceae): cypress crown colonies in southern Florida. *Selbyana* 5: 256-263.
- Carson, H. L. 1970. Chromosome tracers of the origin of species. *Science* 168: 1414-1418.
- 1971. Speciation and the founder principle. *Stadler Genetics Symposia* 3: 51-70.
- 1975. Genetics of speciation at the diploid level. *Amer. Naturalist* 109: 83-92.
- Dayton, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351-389.
- 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.* 45: 137-159.
- Horn, H. S. & R. H. MacArthur 1972. Competition among fugitive species in a harlequin environment. *Ecology* 53: 749-752.
- Hutchinson, G. E. 1961. The paradox of the plankton. *Amer. Naturalist* 95: 137-145.
- Koch, A. L. 1974. Competitive coexistence of two predators utilizing the same prey under constant environmental conditions. *J. Theor. Biol.* 44: 387-395.
- Levins, R. 1968. *Evolution in changing environments*. Princeton Univ. Press, Princeton, N. J.
- MacArthur, R. & R. Levins 1964. Competition, habitat selection, and character displacement in a patchy environment. *Proc. Natl. Acad. Sci. U.S.A.* 51: 1207-1210.
- Madison, M. 1979. Distribution of epiphytes in a rubber plantation in Sarawak. *Selbyana* 5: 207-213.
- Mayr, E. 1942. *Systematics and the Origin of Species*. Columbia Univ. Press, N.Y.
- McGehee, R. & R. A. Armstrong 1977. Some mathematical problems concerning the ecological principle of competitive exclusion. *J. Differential Equations* 23: 30-52.
- Nei, M., T. Maruyama & R. Chakraborty 1975. The bottleneck effect and genetic variability in populations. *Evolution* 29: 1-10.
- Pittendrigh, C. 1948. The bromeliad-Anopheles-malaria complex in Trinidad. I. The bromeliad flora. *Evolution* 2: 58-89.
- Powell, J. R. 1978. The founder-flush speciation theory: an experimental approach. *Evolution* 32: 465-474.
- Root, R. 1967. The niche exploitation pattern of the blue-gray gnatcatcher. *Ecol. Monogr.* 37: 317-350.
- Sale, P. F. 1977. Maintenance of high diversity in coral reef communities. *Amer. Naturalist* 111: 337-359.
- Sanford, W. W. & I. Adanlawo 1973. Velamen and exodermis characters of West African epiphytic orchids in relation to taxonomic grouping and habitat tolerance. *J. Linn. Soc., Bot.* 66: 307-321.
- Volterra, V. 1928. Variations and fluctuations of the number of individuals in animal species living together. *J. du Conseil* 3: 3-51.
- Went, F. W. 1940. Soziologie der Epiphyten eines tropischen Urwaldes. *Ann. Jard. Bot. Buitenzorg* 50: 1-98.